Comparative Evidence that Salt Marshes and Mangroves May Protect Seagrass Meadows from Land-derived Nitrogen Loads

Ivan Valiela* and Marci L. Cole

Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA

ABSTRACT

Seagrass meadows within estuaries are highly sensitive to increased supplies of nitrogen (N). The urbanization of coastal watersheds increases the delivery of N to estuaries, threatening seagrass habitats; both seagrass production per unit area and the area of seagrass meadows diminish as land-derived N loads increase. The damaging effects of land-derived N loads may be lessened where there are fringes of coastal wetlands interposed between land and seagrass meadows. Data compiled from the literature showed that production per unit area by seagrasses increased and losses of seagrass habitat were lower in estuaries with relatively larger areas of fringing wetlands. Denitrification and the burial of land-derived N within fringe wetlands may be sufficient to protect N-sensitive seagrass habitats from the detrimental effects of land-derived N. The protection furnished by fringing wetlands may be overwhelmed by increases in anthropogenic N loads in excess of 20–100 kg N ha^{-1} y^{-1}. The relationships of land-derived N loadings, fringing coastal wetlands, and seagrass meadows demonstrate that different units of the landscape mosaic found in coastal zones do not exist as separate units, but instead are coupled and uncoupled by biogeochemical transformations and transport among environments.

Key words: wetlands; seagrass; nitrogen; salt marshes; mangroves; coastal habitats; nutrient interception.

INTRODUCTION

Land-derived nitrogen (N), largely of anthropogenic origin, is a major agent of change in estuaries and coastal waters world-wide (GESAMP 1990; NRC 1994). Such terrestrial inputs have increased eutrophication in many of the world's shallow coastal waters; one of the consequences of this eutrophication is the loss of ecologically and commercially important seagrass meadows (Valiela and others 1992; Duarte 1995).

The coastlines of the world are bordered by zones of fringing wetlands, such as salt marshes in temperate latitudes and mangroves in the tropics. In general, such wetlands are located between the terrestrial watersheds that are sources of N and the receiving estuarine waters, which are generally subject to eutrophication. Salt marshes and mangroves are sedimentary systems with relatively high rates of denitrification and nitrogen burial (Valiela and Teal 1979; Seitzinger 1988). The specific location of these fringing wetlands—between land and sea—and their relatively high rates of biogeochemical transformations suggest that coastal wetlands may furnish a considerable environmental service, intercepting land-derived N loads before the supply of limiting nutrient reaches and alters the N-sensitive seagrass habitats in the receiving estuaries (Valiela and others 2000).

In this paper, we first confirm the sensitivity of seagrass meadows to N loads and then examine the possible role of coastal fringing wetlands in reducing the effects of terrestrial N loads. To accomplish these two objectives, we compiled the published data to comparatively define the dependency of seagrass habitats on the land-derived N load and then attempted to ascertain how the production and area of seagrass habitats might be related to areas of coastal wetlands.

METHODS

We first compiled the information available in the literature for as many estuarine systems as we could find on annual N loads; seagrass, macroalgal, and phytoplankton production rates; and areas of past and present seagrass (Table 1). N loads are shown as kilograms of land-derived N entering each estuary annually from the watershed, divided by total area of the estuary. The total estuary area was the sum of wetland area and open water area. We calculated the percent of total production carried out by seagrasses in each estuary using data on phytoplankton plus macroalgal production, or total production, depending on what value was given by the sources. Some sources provided estimates of loss of seagrass habitat over recent decades, as shown in Table 1.

Salt marsh and mangrove areas for many estuaries are compiled in Table 2. To estimate the potential interception of land-derived N in the areas of these coastal wetlands, we multiplied the mean values of N losses via denitrification and burial by the area of wetland in each estuary (Table 3). We then compared the estimates of potential losses within the wetlands to the annual land-derived N loads reported in Table 2. This comparison allowed an estimate of the magnitude of land-derived N potentially intercepted by the area of wetland in each estuary.

Many additional variables (water residence times, hypsometry, sediment loads, area of the estuary, and so on) must also affect the status of seagrass meadows. Incidental to the data compilation that produced Tables 1, 2, and 3, we also obtained data, when possible, for these additional variables, which varied broadly among the estuaries in the compilation. We compared eelgrass production and loss to these other variables, as well as to the area of fringing wetlands.

RESULTS

Production and area of seagrass meadows were impaired under increased N loads (Figure 1). Primary production by seagrasses as a percent of total production varied considerably among different estuaries exposed to low land-derived N loads. Percent seagrass production in estuaries subject to lower N loads reached 90%, but the high percentages diminished sharply as land-derived N loads to estuaries increased (Figure 1A).

The high sensitivity of seagrasses to increases in N loads was also evident in data expressed as percent of seagrass habitat lost from the estuaries vs N load received by the estuaries (Figure 1B). Percent seagrass cover lost increased as land-derived N loads increased; nearly the entire seagrass habitat cover was lost in estuaries exposed to land-derived N loads greater than 100 kg N per hectare of estuary per year. These comparative results confirm previous conclusions that seagrasses are sensitive to the N delivery regime (Sand-Jensen and Borum 1991; Valiela and others 1992; Duarte 1995; Short and Burdick 1996).

The more novel result of our comparative synthesis is that nutrient-driven impairment of seagrass meadows diminished in the presence of larger areas of fringing wetland (Figure 2). We arrive at this conclusion from two different analyses of the data. First, production by seagrasses as a percentage of total estuary production increased linearly, nearly 1:1, as the percentage of area in the estuaries that was wetland ([wetland area/total estuary area] 100) increased (Figure 2A). This result suggests that where there were relatively larger areas of coastal wetlands, all other things apart, seagrass production was higher relative to production by phytoplankton and macroalgae.

Second, the relative loss of seagrass cover was significantly smaller in estuaries with relatively larger areas of fringing wetlands (Figure 2B). This result suggests that the extent of the seagrass habitat was linked in some fashion to the area of fringing coastal wetland.

To make sure that the relationship between wetland area and seagrass status was not a spurious relationship, we then plotted seagrass production and seagrass loss vs other estuarine variables in our compilation. Neither seagrass production/total production or percent seagrass cover loss was significantly related to either total estuary size, water residence time, or mean depth (Table 4 and Figure 3). We therefore only found a clear-cut relationship between relative area of wetland and seagrass status.

We also compared the relationship for sediment-laden southern estuaries and clean-water northern systems and found that the wetland to seagrass statistics did not differ. We should add that there

Table 1.   Nitrogen Loads, Seagrass Production as g C m^{-2} y^{-1} and as % of Total Primary Production, Loss of Seagrasses, and Coastal Wetland Area Relative to Total Estuarine Area for Selected Estuaries

	N Load (kg N ha^{-1} y^{-1})	Seagrass Production (g C m^{-2} y^{-1})	(%)	Seagrass Loss (%)	Wetland Area (%)	Reference
Barnegat Bay	5		36		18	Kennish and Lutz 1984
Bass Harbor Marsh	225	46	13			Kinney and Roman 1998
Bassin d'Arcachon	64		69			Castel and others 1996
Biscayne Bay	0		90			Roman and others 1983
Buttermilk Bay	77		44			Buzzards Bay Project, Costa 1988; Valiela and Costa 1988
Charlestown Pond	52	22	15		8	Nixon and Lee 1981; Thorne-Miller and others 1983; Thorne-Miller and Harlin 1984; Lee and Olsen 1985
Charlotte Harbor	42			29	19	Hoffman and Dawes 1997; Tomasko and Hall 1999
Childs River	601		0	100	2	Short and others 1993; Valiela and others 1997a, 1997b
Chincoteague Bay	31		42		34	Orth and others 1992; Eaton and Kimsey 1993; Boynton and others 1996
Cockburn Sound	103			81		Cambridge and others 1986; Cambridge and Hocking 1997
Corpus Christi	13		33		29	Morgan and Kitting 1984
Eel Pond	93			95	15	Short and others 1993; Valiela and others 1997a, 1997b
Ems-Dollard	610	0	3			Nienhuis 1992
Great Bay	252		27		18	Short and Mathieson 1992
Great South Bay	20			53	22	Nixon and others 1994
Green Pond	137			100	5	Kroeger and others 1999
Grevelingen	40	4	18			Nienhuis 1992
Hamblin Pond	15			28	34	Short and others 1993; Valiela and others 1997a, 1997b
Jehu Pond	22			7	52	Short and others 1993; Valiela and others 1997a, 1997b
Laguna Terminos			68		45	Day and others 1982; Deegan and others 1986; Bianchi and others 1999
Langstone Harbor	637			100	10	Tubbs and Tubbs 1983; Lowthion and others 1985; Montgomery and others 1985; den Hartog 1994
Mashpee River	167			100	20	M. L. Cole unpublished
Moreton Bay	24	183	46		6	Hyland and Butler 1988; Hyland and others 1989; O'Donohue and Dennison 1997; O'Donohue and others 2000
Nauset Marsh	11	716	45		35	Roman and others 1990
Oosterschelde	50	0	1		2	Nienhuis 1992
Point Judith Pond	34	175	67			Nixon and Lee 1981; Thorne-Miller and others 1983; Thorne-Miller and Harlin 1984; Lee and Olsen 1985
Potters Pond	94	140	38			Nixon and Lee 1981; Thorne-Miller and others 1983; Thorne-Miller and Harlin 1984; Lee and Olsen 1985
Quashnet River	350		0	100	12	Short and others 1993; Valiela and others 1997a, 1997b
Roskilde Fjord	204	250	34			Nienhuis 1992
Sage Lot Pond	14		45	14	54	Short and others 1993; Valiela and others 1997a, 1997b
Sarasota Bay	56			30	11	Deegan and others 1986; Bianchi and others 1999
Tampa Bay	28			65	6	Deegan and others 1986; Bianchi and others 1999
Timm's Pond	8			17	44	Short and others 1993; Valiela and others 1997a, 1997b
Trustom Pond	40	341	80			Nixon and Lee 1981; Thorne-Miller and others 1983; Thorne-Miller and Harlin 1984; Lee and Olsen 1985
Veerse Meer	340	125	1			Nienhuis 1992
Venice Lagoon	130	600				Sfriso and others 1992; Sfriso and Ghetti 1998
Wadden Sea	500	0	3			Nienhuis 1992

Table 2. Area of Salt Marsh (s) and Mangrove (m), Potential Removal of Land-derived N by Denitrification and Burial, and Land-derived N Loads for Selected Estuaries

	Wetland Type	Wetland Area (ha)	N Removed by Wetlands (kg N y⁻¹)	N Load (kg N y⁻¹)	N Removed by Wetlands (%)	N Load (kg N ha⁻¹ y⁻¹)	Reference
Acushnet River	s	15	2,039	57,579	4	53	Buzzards Bay Project, Costa 1988
Apalachee Bay	s	28,337	3,740,484	3,179,512	118	56	Deegan and others 1986; Bianchi and others 1999
Apalachicola Bay	s	8623	1,138,236	11,383,239	10	147	Deegan and others 1986; Bianchi and others 1999
Apponagansett Bay	s	115	15,140	19,773	77	49	Buzzards Bay Project, Costa 1988
Aucoot Cove	s	53	7036	2516	280	14	Buzzards Bay Project, Costa 1988
Brant Island Cove	s	47	6230	374	1668	5	Buzzards Bay Project, Costa 1988; Valiela and Costa 1988
Buttermilk Bay	s	20	2618	17,434	15	79	Deegan and others 1986; Bianchi and others 1999
Calcasieu River	s	102,073	13,473,636	32,909,184	41	168	Deegan and others 1986; Bianchi and others 1999
Charlotte Harbor	m	26,181	1,319,522	5,823,048	23	42	Hoffman and Dawes 1997; Tomasko and Hall 1999
Childs River	s	0	40	8116	1	601	Short and others 1993; Valiela and others 1997a, 1997b
Choctawatchee	s	1140	150,480	2,525,390	6	70	Deegan and others 1986; Bianchi and others 1999
Clarks Cove	s	0	0	17,131	0	60	Buzzards Bay Project, Costa 1988
East Branch Westport River	s	317	41,844	76,204	55	68	Buzzards Bay Project, Costa 1988
Eel Pond	s	7	948	4502	21	93	Short and others 1993; Valiela and others 1997a, 1997b
Florida Bay	m	86,473	4,358,239	46,479	9377	0	Deegan and others 1986; Bianchi and others 1999; Hall and others 1999
Great South Bay	s	5140	678,480	230,300	295	10	Dennison and others 1987; Nixon and others 1994
Green Pond	s	10	1292	6445	20	137	Kroeger and others 1999
Hamblin Pond	s	20	2614	893	293	15	Short and others 1993; Valiela and others 1997a, 1997b
Hen Cove	s	2	198	3647	5	133	Buzzards Bay Project, Costa 1988
Jehu Pond	s	47	6224	1968	316	22	Short and others 1993; Valiela and others 1997a, 1997b
Laguna Madre	s	101,214	13,360,248	31,660,524	42	126	Deegan and others 1986; Bianchi and others 1999
Marks Cove	s	20	2666	1278	209	19	Buzzards Bay Project, Costa 1988
Mashpee River	s	15	1998	6150	32	167	M.L. Cole unpublished
Matagorda Bay	s	48,582	6,412,824	20,996,514	31	126	Deegan and others 1986; Bianchi and others 1999
Mattapoisett Harbor	s	95	12,500	32,497	38	62	Buzzards Bay Project, Costa 1988
Megansett Harbor	s	1	92	5565	2	33	Buzzards Bay Project, Costa 1988
Mississippi Sound	s	27,087	3,575,484	28,407	12,587	0	Deegan and others 1986; Bianchi and others 1999
Mobile Bay	s	8693	1,147,476	18,220,356	6	147	Deegan and others 1986; Bianchi and others 1999

Table 2. (Continued)

	Wetland Type	Wetland Area (ha)	N Removed by Wetlands (kg N y^{-1})	N Load (kg N y^{-1})	N Removed by Wetlands (%)	N Load (kg N ha^{-1} y^{-1})	Reference
Moreton Bay	m	9500	478,800	3,624,740	13	24	Hyland and Butler 1988; Hyland and others 1989; O'Donohue and Dennison 1997; O'Donohue and others 2000
Nasketucket Bay	s	119	15,695	10,851	145	34	Buzzards Bay Project, Costa 1988
Onset Bay	s	73	9676	10,150	95	33	Buzzards Bay Project, Costa 1988
Pensacola Bay	s	4216	556,512	8,255,016	7	126	Deegan and others 1986; Bianchi and others 1999
Perdido Bay	s	433	57,156	1,142,988	5	154	Deegan and others 1986; Bianchi and others 1999
Phinneys Harbor	s	30	3907	6732	58	27	Buzzards Bay Project, Costa 1988
Quashnet River	s	3	436	9879	4	350	Short and others 1993; Valiela and others 1997a, 1997b
Quissett Harbor	s	2	277	1340	21	27	Buzzards Bay Project, Costa 1988
Red Brook Harbor	s	7	898	2576	35	38	Buzzards Bay Project, Costa 1988
S. Ten Thousand Islands	m	72,095	3,633,588	479,199	758	4	Deegan and others 1986; Bianchi and others 1999
Sabine Estuary	s	126	16,632	5,015,304	0	126	Deegan and others 1986; Bianchi and others 1999 Short and others 1993; Valiela and others 1997a, 1997b
Sage Lot Pond	s	15	2017	400	504	14	Deegan and others 1986; Bianchi and others 1999
Sarasota Bay	m	1647	83,009	879,984	9	56	Deegan and others 1986; Bianchi and others 1999
Sippican Harbor	s	67	8844	4953	179	6	Buzzards Bay Project, Costa 1988
Squeteague Harbor	s	1	92	3620	3	118	Buzzards Bay Project, Costa 1988
St. Andrew Bay	s	21,017	2,774,244	3,364,732	82	49	Deegan and others 1986; Bianchi and others 1999
Suwanee River	s	13,114	1,731,048	20,438,600	18	700	Deegan and others 1986; Bianchi and others 1999
Tampa Bay	m	8517	429,257	3,706,416	12	28	Deegan and others 1986; Bianchi and others 1999 Short and others 1993; Valiela and others 1997a, 1997b
Timms Pond	s	3	436	60	726	8	
Wareham River	s	97	12,857	48,496	27	140	Buzzards Bay Project, Costa 1988
West Branch Westport River	s	104	13,788	24,567	56	39	Buzzards Bay Project, Costa 1988
West Falmouth Harbor	s	16	2072	3031	68	32	Buzzards Bay Project, Costa 1988
Weweantic River	s	95	12,553	112,988	11	339	Buzzards Bay Project, Costa 1988
Widows Cove	s	16	2046	257	796	4	Buzzards Bay Project, Costa 1988
Wild Harbor	s	17	2204	4264	52	65	Buzzards Bay Project, Costa 1988
Wings Cove	s	15	2020	1136	178	11	Buzzards Bay Project, Costa 1988

Table 3. Denitrification and Burial Rates Measured in Wetland Sediments

	Rate (kg N ha^{-1} y^{-1})	Reference
Salt marsh denitrification	78.5	Kaplan and others 1979
	92.0	White 1994
	120.5	Haines and others 1977
	10.2	Abd Aziz and Nedwell 1986
	76.1	Koch and others 1992
	12.6	Joye and Paerl 1994
	9.5	Thompson and others 1995
Mangrove denitrification	7.3	Corredor and others 1999
	7.9	Corredor and others 1999
	4.4	Corredor and others 1999
	6.6	Corredor and Morell 1984
	22.9	Corredor and Morell 1984
	14.8	Rivera-Monroy and Twilley 1996
	0.0	Rivera-Monroy and Twilley 1996
	0.4	Rivera-Monroy and Twilley 1996
	0.3	Rivera-Monroy and Twilley 1996
	0.2	Kristensen and others 1998
	4.0	Nedwell and others 1994
Salt marsh burial	37	White 1994
	41	Valiela and Teal 1979

was no significant relationship between land-derived N load and percent wetland area ($r = 0.36$, ns), so there was no issue of colinearity among these two presumed independent variables (Petraitis and others 1996).

In our analysis, we did not ignore the other estuarine variables; we merely asked whether we could see significant relationships between areas of wetlands and seagrass survival that emerged above the scatter created by the many additional variables. This is both a weakness and an advantage of the comparative approach we employed. The weakness is that it is difficult to identify cause–effects given the large scatter of the data; the advantage is that we can compare many and diverse systems. The overall result of the data compilation in Figures 1 and 2 was that both productivity and areal cover by seagrass meadows seemed significantly impaired by larger land-derived N loads to the estuary, but the detrimental effect was lower where relative area of coastal fringing wetlands was larger.

DISCUSSION

The mechanisms underlying the effects of N loads that we report in Figure 1 are reasonably well understood: Seagrasses are highly sensitive to reductions in light availability (Dennison and Alberte 1982; Zimmerman and others 1987), and increased

N loads indirectly lower the light supply as they increase the biomass of phytoplankton (Tomasky and others 1999), macroalgae (Hauxwell and others 1998), and epiphytes (Borum 1985), all of which intercept light that would otherwise reach the seagrasses. In particular, in our Cape Cod work, we found that land-derived N loads to the estuary in excess of 20–30 kg N ha^{-1} y^{-1} were sufficient to decrease seagrass cover, production, and the extent of meadows (Hauxwell 2001; Hauxwell and others 1998). From our compilation of data from a wider variety of geographical sites (Figure 1B), we concluded that there was a 50%–100% reduction in seagrass production and habitat area as land-derived N loads exceed 100 kg N ha^{-1} y^{-1}. Land-derived N loads from 20 to 100 kg N ha^{-1} y^{-1} therefore seem to be a critical range for seagrass meadows in shallow coastal waters.

The identity of the mechanism underlying the possible mitigating effect of coastal wetlands is less well established. We, and others, conjecture that denitrification and N burial rates in fringing wetlands (Seitzinger 1988) may be high enough to intercept some considerable portion of land-derived N loads (Corredor and Morell 1994; Rivera-Monroy and others 1995, 1999; Rivera-Monroy and Twilley 1996).

To assess whether it is at all reasonable to think that the interception of land-derived N by fringing
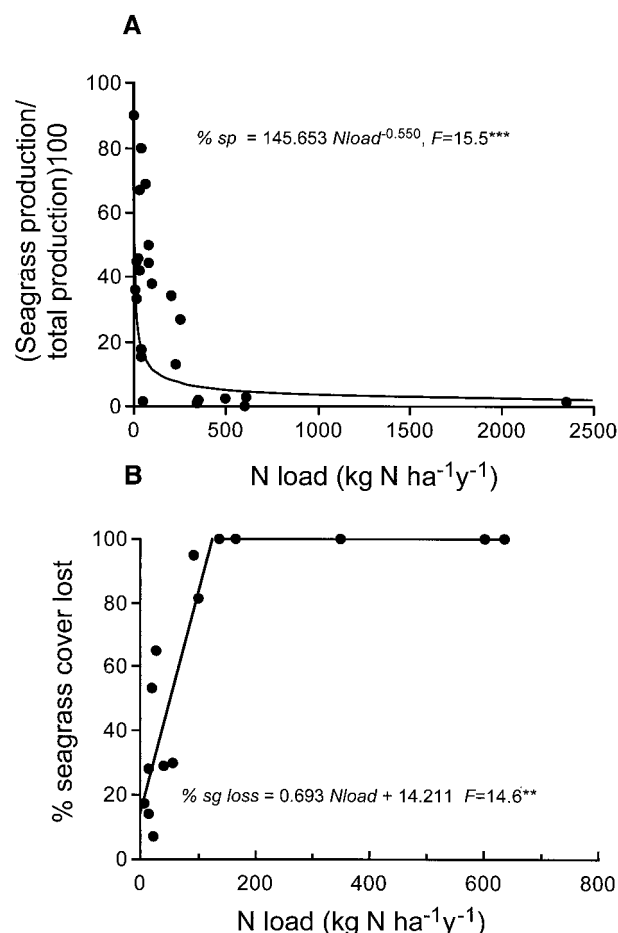
A

$$\% sp = 145.653\ Nload^{-0.550},\ F=15.5^{***}$$

N load (kg N ha^{-1}y^{-1})

(Seagrass production/total production)100

B

$$\% sg\ loss = 0.693\ Nload + 14.211\ \ F=14.6^{**}$$

N load (kg N ha^{-1}y^{-1})

% seagrass cover lost

A

$$\% sg\ pro = 1.117(\%wetland) + 2.668\ \ F=33.5^{***}$$

1:1 line

(Wetland area/total estuary area)100

(Seagrass production/total production)100

B

$$\% sg\ lost = 118.130 \bullet 10^{-0.019(Nload)}\ \ F=6.7^{*}$$

(Wetland area/total estuary area)100

% seagrass cover lost

Figure 1. (A) Seagrass production and percent seagrass production as percent of total production vs land-derived nitrogen load to the estuary. (B) Percentage of area of seagrass habitat lost (over last 10–30 years) in several estuaries plotted vs the corresponding land-derived N load. Data from Table 1. $**P < 0.01$; $***P < 0.001$.
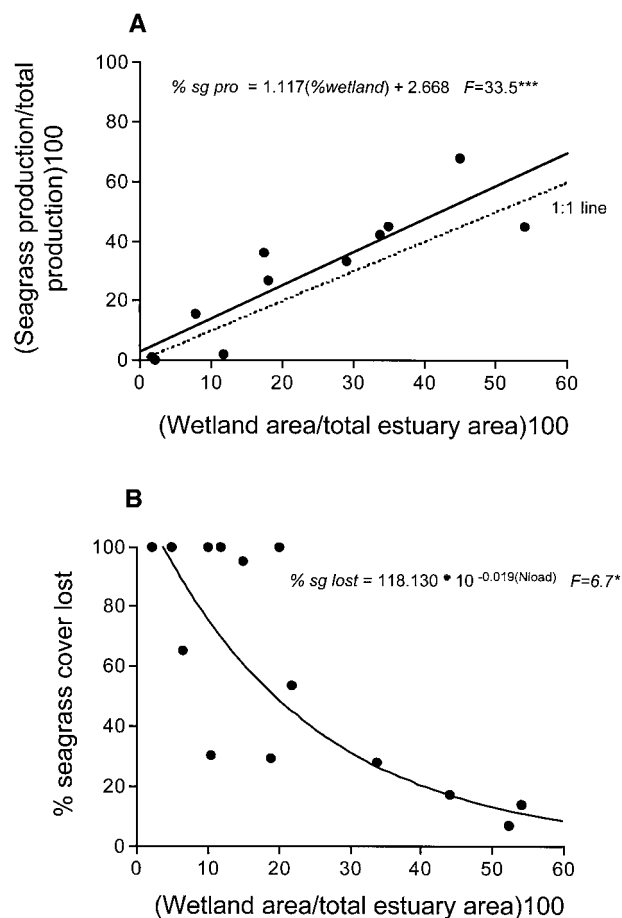
Figure 2. (A) Seagrass production expressed as percent of total production in many estuaries plotted vs the area of fringing wetland expressed as percent of total estuary area. (B) Percent of area of seagrass habitat lost (over last 10–30 years) plotted vs the percent of area of the estuary made up by fringing wetland. Data from Table 2. $*P < 0.05$; $***P < 0.001$.

wetlands might be quantitatively significant as a mechanism permitting seagrass survival, we used available data on the rates of denitrification and N burial (Table 3), area of wetland (Table 2), and land-derived N loads (Table 2) for as many sites as we could find in the literature. With these data, we calculated the potential loss of land-derived N that might take place as the N traveled from land through the fringing coastal wetlands on its way to the deeper waters. We simply wanted to see if the interception was likely to be large enough to matter.

The ratio of land-derived N to potential loss in the wetlands ranged from small fractions to many-fold (Figure 4A). The differences depended on the dimensions of the wetland relative to those of the estuary. Our calculation assumed that denitrifica-

tion and burial rates did not change as N loads change, but denitrification rates may increase as the availability of nitrate increases (Seitzinger 1988), so our values may underestimate actual rates.

There was broad variation in the potential interception of terrestrial N within the wetland fringe of the various estuaries. To avoid the influence of the high values, we can focus on the median interception, which was 27% of the land-derived loads (Figure 4A). The sensitivity of seagrasses to N loads may be high enough that this interception could be sufficient to furnish a measure of protection to seagrass meadows. We know that even smaller changes have biological consequences. Subtle but consistent changes, such as a 2°C change in mean global temperature or a 1–2 cm rise in sea level,

Table 4. Results of Regression analyses of Seagrass Loss and production in Relation to Total Area of the Estuaries, Water Residence Time, and Mean Depth

	% Seagrass Cover Loss			% Seagrass Production		
	n	F	R^2	n	F	R^2
Variable						
Total estuary area (ha)	17	1.60 ns	0.096	24	0.28 ns	0.013
Water residence time (d)	13	0.05 ns	0.050	24	0.37 ns	0.004
Mean depth (m)	13	0.03 ns	0.003	13	0.76 ns	0.087

n, number of estuaries; F, F ratio for regressions; R^2, coefficient of determination; ns, not significant
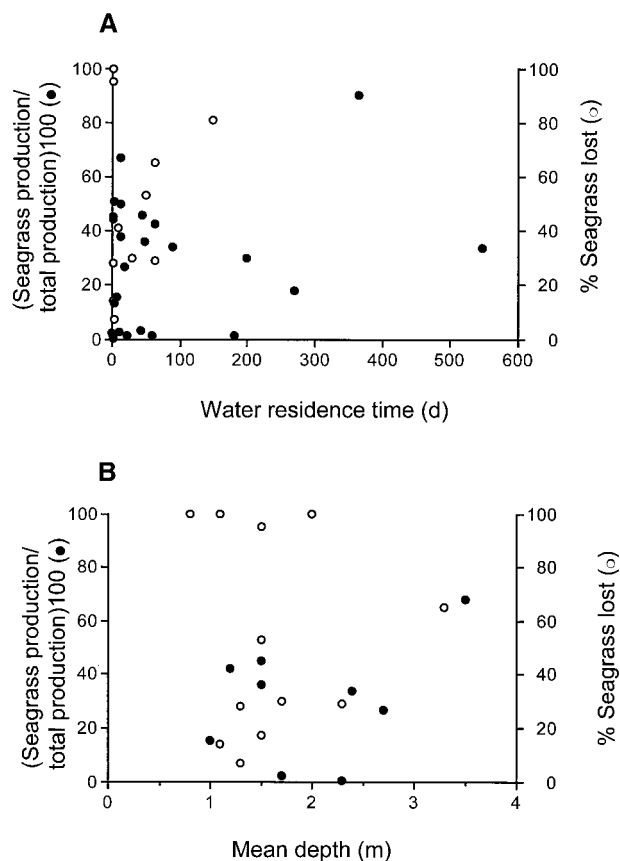
Figure 3. (A) Seagrass production expressed as percent of total production and percent seagrass cover loss in many estuaries plotted vs water residence time expressed in days. (B) Percent seagrass production and seagrass habitat lost (over last 10–30 years) plotted vs mean water depth expressed in meters.

Figure 4. (A) Frequency distribution of values for percent land-derived N load (in kg y^{-1} for the entire watershed) that is potentially removed within fringing wetlands by denitrification and burial in each of many estuaries. Black bars refer to salt marshes (sm); white bars refer to mangrove swamps (m). (B) Estimates of potential interception of land-derived loading (in rates of kg N y^{-1}) plotted vs land-derived N load expressed as a per unit of estuary area basin (kg N ha^{-1} y^{-1}). The gray area shows the "critical" range of land-derived N loads for seagrass meadows. Data from Table 2.

have been repeatedly shown to have significant biological effects.

We should note that it was not our intent here to balance the many important N inputs and outputs that occur within estuaries, such as denitrification, burial, N fixation in bare sediments, particle transport, tidal exchanges, and other processes that
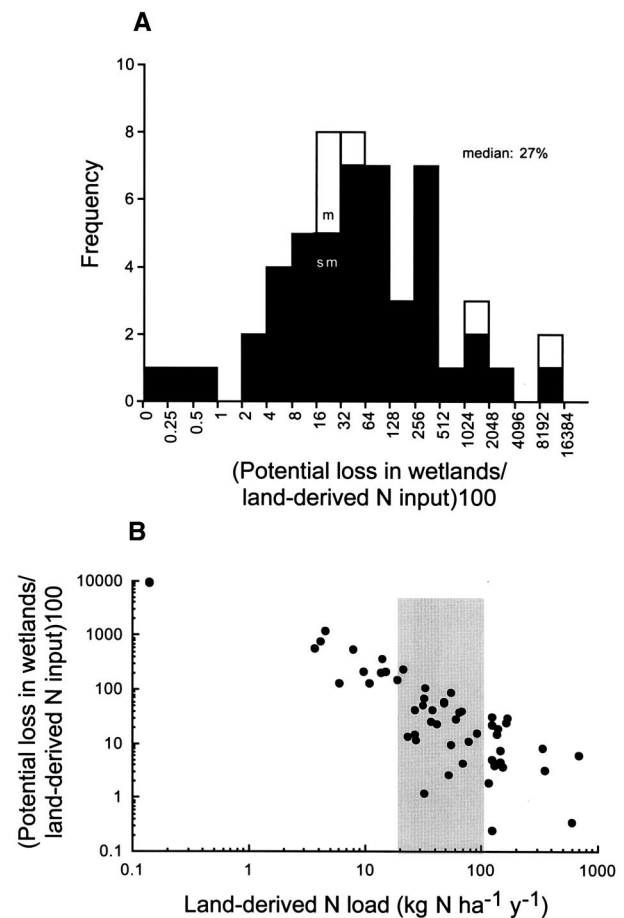
occur in different parts of estuaries. Such an N budgeting for each estuary is beyond the scope of this paper. Rather, in compiling Figure 4 we limited ourselves to considering whether the potential losses of available N within the wetland fringe—the portion of estuarine habitat that is positioned to first receive land-derived N inputs—might be of a magnitude that would reasonably affect the throughput of terrestrial N to the seagrass habitats down-estuary, so that it might be reasonable to suggest that the interaction was a mechanism underlying the relationships shown in Figure 2.

Potential percent removal was lower where anthropogenic sources have added to the N loads (Figure 4B). Across the critical range of loads that we found impaired seagrasses ($20–100 \text{ kg N ha}^{-1} \text{ y}^{-1}$ on the x-axis of Figure 4B), wetlands may intercept anywhere from nil to more than 100% of the land-derived N load (Figure 4B). Beyond $100 \text{ kg N ha}^{-1} \text{ y}^{-1}$, retention in the fringing wetlands was less than 10% (Figure 4B). This suggests that the natural water quality "subsidy" that results from the fringing marshes may be overwhelmed by high loads that can be generated by changes in land use on coastal watersheds. Where N loads are lower than $100 \text{ kg N ha}^{-1} \text{ y}^{-1}$, however, fringing wetlands may retain sufficient land-derived N to protect seagrass meadows. We note that 67% of the sites included in Figure 4B are exposed to land-derived N loads of less than $100 \text{ kg N ha}^{-1} \text{ y}^{-1}$. This means that in about two-thirds of the reported cases, coastal wetlands contributed a possible benefit for seagrass meadows.

The exchanges between terrestrial land-use mosaics, fringing wetlands, and seagrass meadows that are implied by our results suggest that adjoining parcels of land and waterscapes are not isolated units. Rather, recognizably different ecosystems, each with distinctive fauna and flora, are connected to one another. In our case, the transport of N from land links—and influences to some degree—conditions in seagrass ecosystems. If a sufficient area of fringing wetland is interposed between land and seagrass meadow, the linkage may be mediated by biogeochemical transformations within the fringing wetlands; but as anthropogenic activities on land increase, the land-derived N loads may overwhelm the ability of wetlands to protect N-sensitive seagrass meadows. In many parts of the world, there have been extensive losses of areas of coastal wetlands by habitat destruction (Mitsch and Gosselink 2000; Valiela and others Forthcoming). Where wetlands have been lost, it is also likely that protective subsidies provided by these wetlands have also been lost.

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